Herbivores regulate the sensitivity of soil organic carbon decomposition to warming

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Abstract

There is considerable interest in how the sensitivity of soil organic carbon (SOC) decomposition to warming is determined by the degree of recalcitrance (i.e., quality) of SOC. Although herbivores have widespread effects on the quality of plant litter, from which SOC is derived, herbivores are seldom considered in studies that examine the response of SOC degradation and greenhouse gas emissions to warming. In this study, we addressed the question: do herds of wild ungulates affect the temperature sensitivity of SOC decomposition in grasslands of Yellowstone National Park (YNP)? We examined the effects of ungulates on temperature sensitivity by comparing microbial respiration at different temperatures in incubated soils collected inside and outside long-term ungulate exclosures. Exclosure sites included grasslands on hilltops, slopes, and at the base of slopes that varied considerably in soil properties. Herbivores reduced the temperature sensitivity of SOC decomposition uniformly among sites by 20% ($P = 0.002$). The herbivore—induced decline in temperature sensitivity was probably governed by YNP grazers increasing the quality of grassland SOC. Results from this study suggest that herbivores regulate how global warming modifies grassland SOC decomposition, stability, and CO_2 emissions.

Keywords: global warming, grassland, herbivory, soil organic carbon, temperature sensitivity, ungulate, Yellowstone National Park

S Online supplementary data available from stacks.iop.org/ERL/8/044013/mmedia

1. Introduction

Understanding the factors that regulate the temperature sensitivity of soil organic carbon (SOC) decomposition to warming is critical for predicting the stability of the global SOC pool, future atmospheric CO_2 concentrations, and the strength of terrestrial feedbacks that are expected to accelerate climate change. Much recent, often high profile (e.g., Knorr *et al* 2005, Craine *et al* 2010, Mahecha *et al* 2010) attention has focused on how closely temperature sensitivity of SOC decomposition follows the principles of

enzyme kinetics described in the Arrhenius (1889) equation, which predicts that temperature sensitivity will increase with the activation energy (E_a) of a reaction. By extension then, temperature sensitivity of decomposition of recalcitrant material with greater E_a should be greater than labile material associated with lower E_a. Indeed, in the majority of soil incubation studies that examine the temperature sensitivity of decomposition, recalcitrant material is more sensitive to increasing temperature than labile material (Craine *et al* 2010, Conant *et al* 2011).

Herbivores have major and widespread effects on the chemical composition and decomposability of plant litter (Bardgett and Wardle 2003, Pastor *et al* 1993), from which SOC is formed. Ungulates change the quality of plant litter largely by shifting the species composition of ecosystems (Díaz *et al* 2007). Because well over 50% per cent of

the earth's land surface is chronically grazed or browsed by wild or domesticated ungulates (Menke and Bradford 1992, Díaz *et al* 2007), herbivores likely play an important role in governing the global C cycle. However, the effects of herbivores on the temperature sensitivity of SOC decomposition have largely been ignored in climate change studies (Estes *et al* 2011).

The goal of this study was to explore if herbivores control how soil C loss will respond to global warming by determining if grazing ungulates influence the temperature sensitivity of SOC decomposition in a temperate grassland ecosystem in Yellowstone National Park (YNP). Previously (Frank and Groffman 1998), Yellowstone ungulates were found to increase the quality of the SOC pool, indexed as the rate of soil C respired early in a 62 wk laboratory soil incubation when respired C was dominated by the metabolism of labile C. Based on those results and the reaction kinetics related to lower E_a of labile compared recalcitrant SOC, we hypothesized that Yellowstone ungulates reduce temperature sensitivity of SOC decomposition.

2. Methods

2.1. Study area

We examined how large herbivores influenced the temperature sensitivity of soil C respiration on the northern winter range of YNP (44°55′ and 45°10′N and 110°10′ and 110°50′W). The core northern winter range is a 100 000 ha area of mostly rolling shrub–grassland that is grazed by herds of elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*). Herd sizes have fluctuated since after the exclosures used in this study were erected in 1958 and 1962. The northern range elk population (i.e., winter counts) varied 12 859–19 045 for the 15 years before wolf reintroduction in 1995 (Taper and Gogan 2002), after which elk numbers declined to a low of 6070 in 2010 (Wallen 2012), when soils for this study were collected. The northern range bison and pronghorn herds during 1980–2010 ranged 455–2245 and 196–297, respectively (Wallen 2012). Ungulate grazing does not influence which plant species dominate Yellowstone grassland (Houston 1982, Frank and McNaughton 1992), but often affects the number and abundance of less common dicot species (Frank 2005, Frank personal observation).

Soils in YNP were formed during multiple glaciations on tertiary volcanic material (Keefer 1972). YNP's climate consists of a short, dry summers and extended, cold winters. The thirty-year (1977–2007) average temperature and precipitation at Mammoth Hot Springs, located on the northern winter range, were 4.9 °C and 370 mm, respectively.

2.2. Soil sampling

We collected soil from six paired 8 m × 8 m grazed and fenced, ungrazed plots located at different topographic positions. Paired-plots at each site had the same slope and aspect and were located 20–30 m from each other. At each plot, six 0–15 cm deep soil samples were randomly collected using

a 5 cm diameter soil auger. Surface litter and vegetation were removed prior to sampling. The samples were dried at 85 °C for 48 h and shipped to Syracuse University, Syracuse, NY. Soils were passed through a 1 mm sieve and picked clean of roots and rocks. The six replicate samples collected from each plot were combined to form one homogenized sample. Carbon content was determined on a NC 2100 soil CN analyzer (CE instruments) and bulk density and soil texture were determined using standard methods (Elliot *et al* 1999).

2.3. Soil incubations

Soil for each plot was divided into 18 one-pint mason jars of equal mass and wet to 120% of the dry soil weight, the average soil moisture levels during the snow free season found among similar YNP grasslands in previous studies (Frank and McNaughton 1992, Frank and Groffman 1998). Thirty-five or 45 g of soil was added to each jar, depending on the mass of soil collected from each plot. Soils were incubated at 22 °C. Yellowstone ungulates have no effect on soil temperature measured in the field (Risch *et al* 2007). Microbe-respired CO_2 was trapped in 2 ml of 2N NaOH in 20 ml vials placed in each chamber and the CO_2 dissolved in traps was determined using methods of Snyder and Trofymow (1984). Soils were initially incubated for three days to build up the microbial populations, after which microbial respiration was determined during 4–7 day long intervals beginning days 3, 10, 14, and 21, and during 14-day intervals beginning days 28, 42, 56, 70, and 173 of the incubation experiment. Jars were tightly sealed during periods that respiration rates were measured, and capped loosely at other times. Each mason jar was thoroughly vented and evaporated water (determined by change in initial weight) was added back weekly or immediately prior to jars being sealed for measuring respiration. Six of the 18 replicate chambers for each plot were shifted to 27 °C for a seven-week period starting on day 21. Six 'blank' jars containing a base trap and no soil were used to measure background CO_2 capture. Temperature sensitivity of soil C respiration was quantified as the percentage increase of soil respiration at 27 °C relative to the respiration at 22 °C.

2.4. Statistical analyses

The effect of herbivores on respiration at 22 °C during the soil incubation was examined with repeated measures ANOVA. We used linear regression to examine the relationship between temperature sensitivity and soil respiration at 22 °C, an index of the decomposability of SOC.

Study sites varied in topographic position (see the supplemental material, available at stacks.iop.org/ERL/8/044013/mmedia), which is a major determinant of a variety of plant and soil properties in YNP grassland, including plant production, plant community composition and soil C and N concentrations. Consequently, the effect of herbivores on temperature sensitivity was determined with a paired *t*-test ($df = 5$), which controlled for topographic effects on soils.
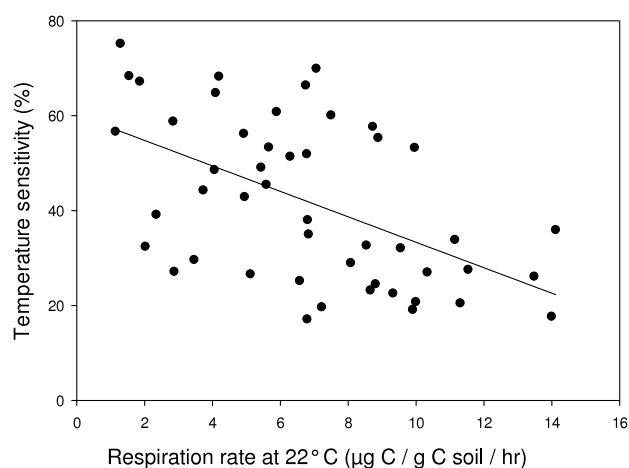
Figure 1. The relationship between temperature sensitive and soil respiration at the 22 °C reference rate for grazed and ungrazed grassland. Each sample point represents the average among replicates during a 7 or 14-day long sampling period.
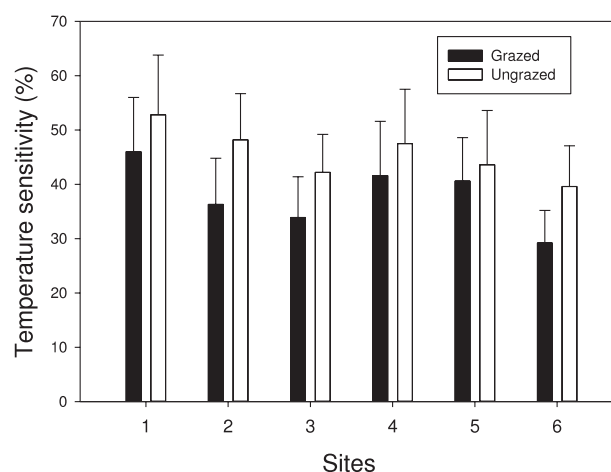

Figure 2. Temperature sensitivity for grazed and ungrazed grassland at six grasslands in Yellowstone National Park. Values are the weighted seven-week means (and standard errors) calculated from one, one-week and three two-week sampling periods. Site properties are described in the supplemental material (available at stacks.iop.org/ERL/8/044013/mmedia).

3. Results

Microbial respiration for soils incubated at 22 °C declined rapidly to a quasi-steady state by day 70 for both grazed and ungrazed soils (see the supplemental material). Herbivores had no effect on 22 °C respiration rate during the period prior to steady state ($P = 0.57$), when the labile SOC was exhausted, or for the entire 173-day lab incubation ($P = 0.81$). Plotting temperature sensitivity (TS) against the reference respiration rate at 22 °C (R22) for all soils (grazed and ungrazed) and time points revealed that temperature sensitivity increased with SOC recalcitrance, i.e., declining respiration (figure 1) (TS $= 60 - 3$[R22]; $r^2 = 0.28$, $P < 0.0001$). There was no relationship between temperature sensitivity and soil C concentration for grazed ($P = 0.21$) or ungrazed ($P = 0.20$) soil, indicating that temperature sensitivity was unrelated to soil C stock size, which in YNP increases downslope from hilltop to slope-bottom positions (see the supplemental material and Frank 2008). Herbivores reduced the seven-week temperature sensitivity of soil respiration among sites by an average of 20% (paired *t*-test, $P = 0.002$) (figure 2). The magnitude that grazers reduced temperature sensitivity was unrelated to grazed and ungrazed soil C concentration ($P = 0.32$), indicating that the grazer effect on temperature sensitivity did not vary across topography positions.

4. Discussion

Increasing temperature sensitivity with increasing SOC recalcitrance, indexed with the respiration at the 22 °C reference temperature (figure 1), is consistent with kinetic theory (Arrhenius 1889) and a number of previous reports (e.g., Fierer *et al* 2005, Conant *et al* 2008, Craine *et al* 2010). In an earlier YNP study (Frank and Groffman 1998), Yellowstone ungulates increased respiration rates early during the soil incubations. Thus we hypothesized that ungulates

would reduce the temperature sensitivity of soil respiration in this study, which was confirmed (figure 2). It was somewhat surprising, however, that ungulates in this study promoted temperature sensitivity while not affecting reference respiration, suggesting that reference microbial respiration rate may be an imperfect measure of SOC properties determining sensitivity to increasing temperature. The lack of an ungulate effect on soil C respiration, in contrast to previous findings that they increased rates (Frank and Groffman 1998), may have been due to the much lower ungulate densities that occurred when soils were collected for this study.

There are several pathways by which ungulates can change SOC quality. First, ungulates increase SOC quality by adding urine and manure to soil. Second herbivory increases the rate of grass root exudation of a variety of compounds such as sugars, carbohydrates, and amino acids that are readily accessible to rhizospheric microbes (Hamilton and Frank 2001, Bardgett and Wardle 2003, Frank and Groffman 2009). Third, herbivory shifts species composition. In resource-rich grasslands under moderate grazing regimes, herbivores increase the abundance of relatively palatable and decomposable forages that facilitate decomposition (Díaz *et al* 2007, Milchunas *et al* 1988, Frank and Groffman 1998, Bakker *et al* 2009). In contrast, in resource poor grassland or under excessive grazing pressure, ungulates often increase the abundance of relatively unpalatable forage species with recalcitrant litter that degrades more slowly (Augustine and McNaughton 1997, Pastor *et al* 1993, Díaz *et al* 2007).

We are aware of only one other study that examined the effects of herbivores on temperature sensitivity of SOC decomposition. In contrast to our results, Paz-Ferreiro *et al* (2012) reported that sheep grazing increased temperature sensitivity of grassland at the Ingleborough National Nature Reserve (INNR) in northern England. Although both studies assessed temperature sensitivity using soil laboratory incubations, Paz-Ferreiro *et al* (2012) incubated intact cores,

while we removed roots and sieved soil prior to incubations. Thus a portion of the temperature sensitivity response measured with the intact cores was due to temperature effects on decomposing roots, which was not a factor in our study. Second, because soil aggregates were broken up during sieving in our experiment, C that had been protected in aggregates contributed to the temperature sensitivity response in our study, and did not in Paz-Ferreiro *et al* (2012). Finally, grazing intensities likely were quite different in the two studies. Stocking rates used by Paz-Ferreiro *et al* (2012) were about 196 kg sheep mass ha^{-1} ((Newland 2012), INNR). In contrast, YNP grassland supports approximately 37 kg ungulate mass ha^{-1} (Frank *et al* 1998). But the most important message from these two studies conducted on different continents, under different grazing pressures, and examining effects of native versus domesticated ungulates was the similar conclusion that large herbivores influenced the temperature sensitivity of SOC decomposition. Taken together, these results suggest that herbivores play a role in the response of grassland soil C stocks to global warming.

The early steep decline in respiration that occurred in both grazed and ungrazed soils (see the supplemental material) is a common pattern observed in lab incubations across many types of soils (Stanford and Smith 1972, Nadelhoffer 1990, Zak *et al* 1994) and reflects the rapid metabolic loss of the relatively small labile SOC pool. Because measurements were made before steady state rates were reached, the results in this study predominately reflected the temperature sensitivity of <10% of the soil C pool. The great bulk of SOC represents older, more recalcitrant material in the slow and passive SOC pools whose turnover dynamics and temperature sensitivities will largely determine the terrestrial feedback of warming on climate. Kinetic theory (Arrhenius 1889) and experimental results (Knorr *et al* 2005, Karhu *et al* 2010) indicate that slow and passive SOC that turns over on decadal to millennial time-scales is more temperature sensitive than active SOC. Little is known about how ungulates affect the long time-scale dynamics of the relatively large pool of old SOC. The single study that we are aware of that examined consumer effects on slow and passive soil C pools used soil radiocarbon measurements to examine long time-scale soil C dynamics in YNP (Frank *et al* 2011). Those findings indicated that YNP ungulates changed the mean turnover period of slow and passive SOC by hundreds of years. Based on the widespread effects that ungulates have on plant litter quality and the rates of soil C processes in other grassland and forest ecosystems (e.g., Pastor *et al* 1993, Bardgett and Wardle 2003, Frank 2008), we suspect that herbivores also have important effects on the long time-scale SOC dynamics and the temperature sensitivity of decomposition of old SOC in other ecosystems, in addition to YNP.

Findings of this study indicate that ungulates reduce the temperature sensitivity of SOC decomposition in grasslands of YNP. These results together with earlier findings (Frank *et al* 2011) that ungulates change the long time-scale turnover rates of slow and passive pools of soil C in YNP, suggest that herbivores play an important role in stabilizing YNP soil C and will be important determinants in future source—sink dynamics of these grasslands as the earth warms. Ungulates occupy over 50% of the terrestrial surface area, where they have profound effects on terrestrial processes. The influence of these animals on how the global C cycle will respond to rising temperatures needs to be better understood.

Acknowledgments

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